Vision with Jittering Eyes

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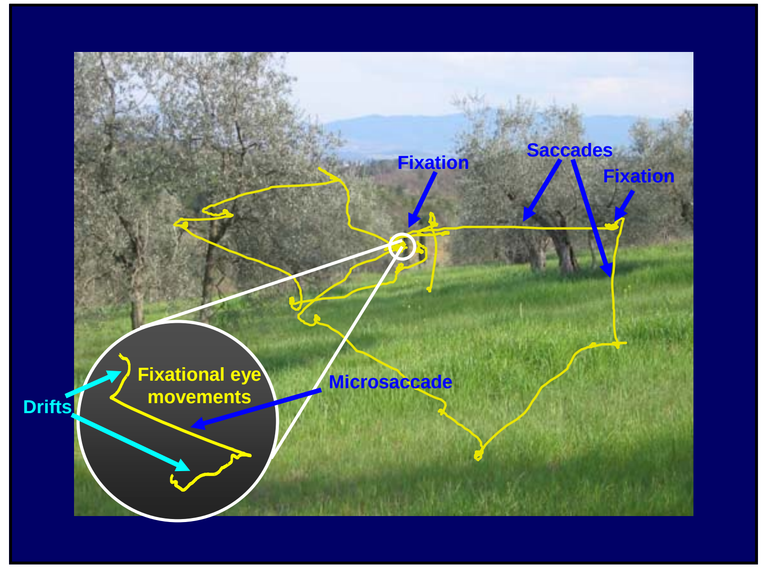
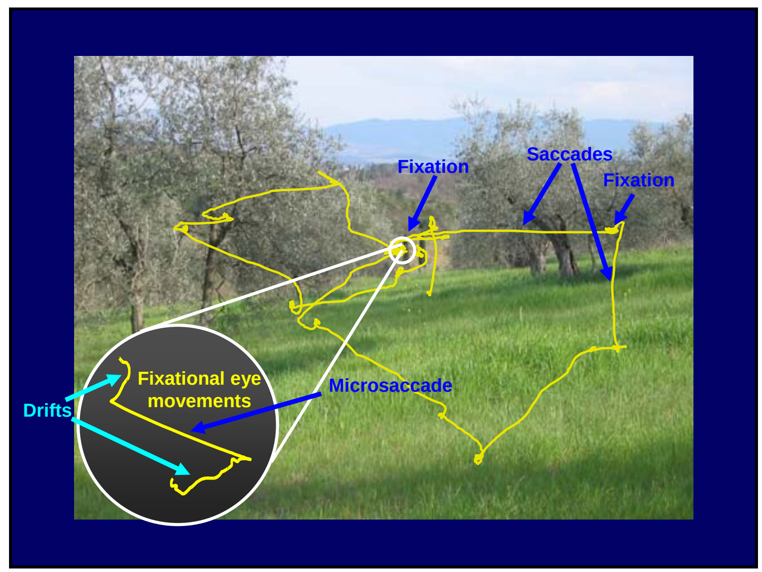
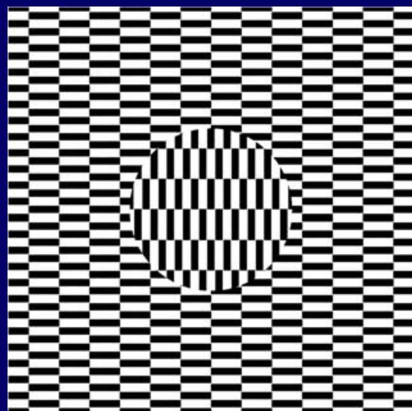
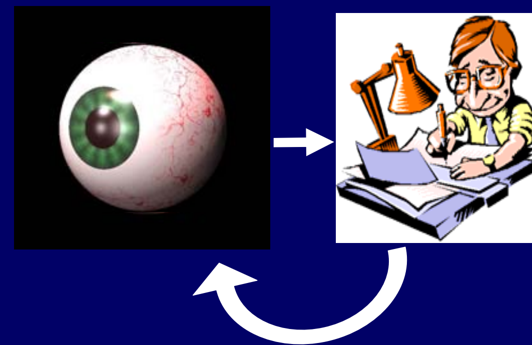




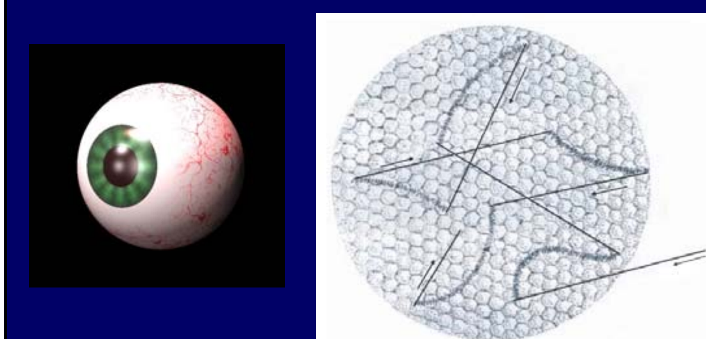


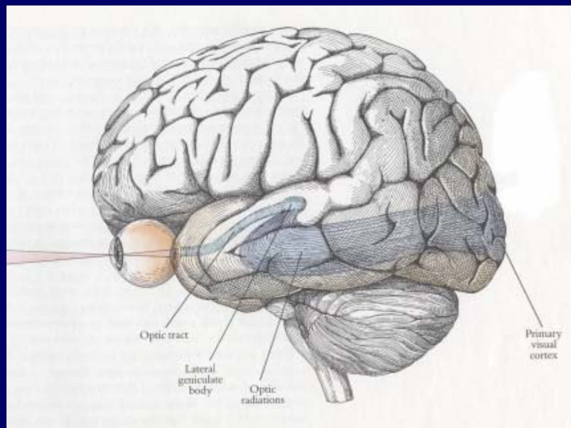
Ouchi, 1997

Active vs. Passive Vision

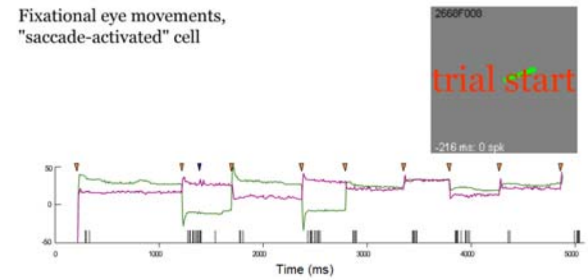


Why do we have fixational eye movements?



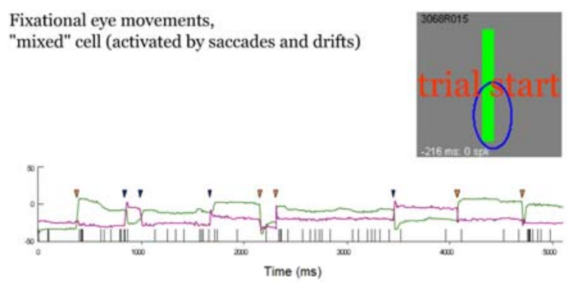


Fixational eye movements modulate cortical activity

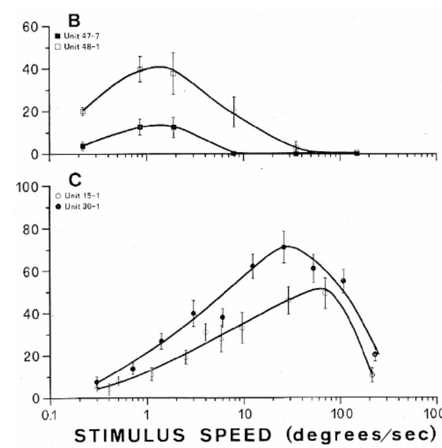


Snodderly, Kagan, and Gur (2002).

Fixational eye movements modulate cortical activity



Snodderly, Kagan, and Gur (2002).

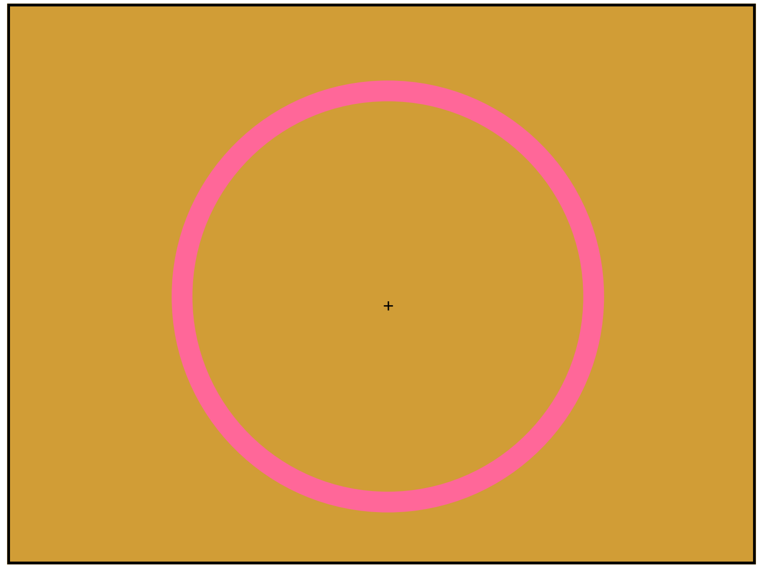


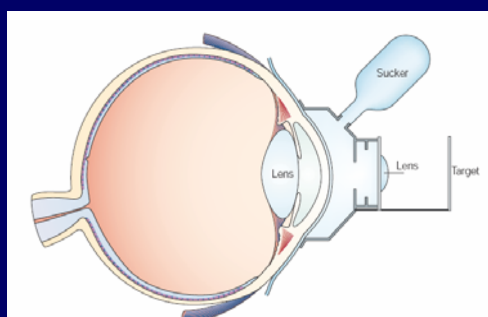
Galletti et al., 1979

Visual functions of fixational eye movements

Many theories have been proposed:

- Refreshing of neural activity. Retinal image motion is needed to prevent the fading of a stationary scene.





The suction cup technique used by Yarbus and others (from Martinzez-Conde et al., 2004).

Visual functions of fixational eye movements

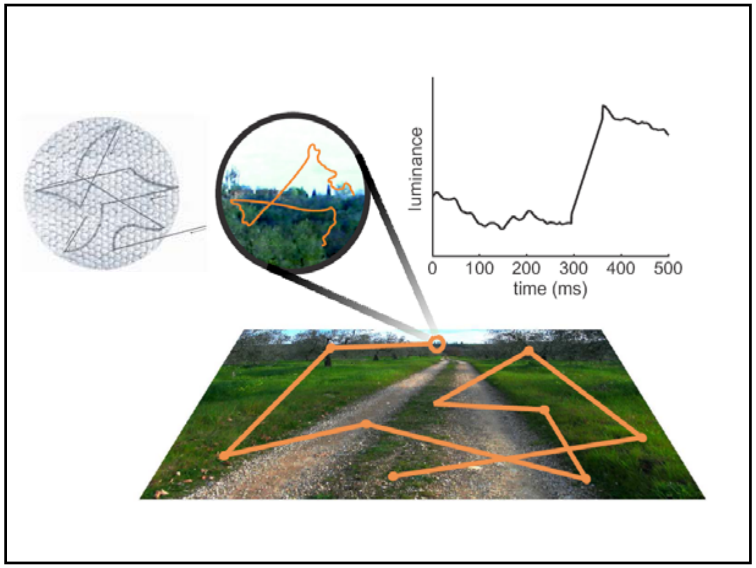
Many theories have been proposed:

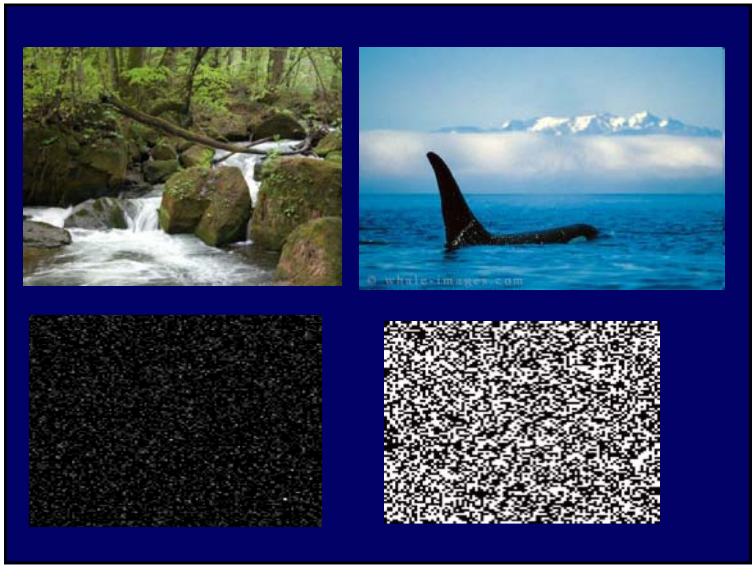
- Refreshing of neural activity. Retinal image motion is needed to prevent the fading of a stationary scene.
- Dynamic theory of visual acuity (Marshal and Talbot, 1942).
- Temporal coding of spatial visual information (Ahissar and Arieli, 2001).
- Dynamic Decorrelation. Fixational instability equalization of spatial frequency contributions with naturalistic stimuli.

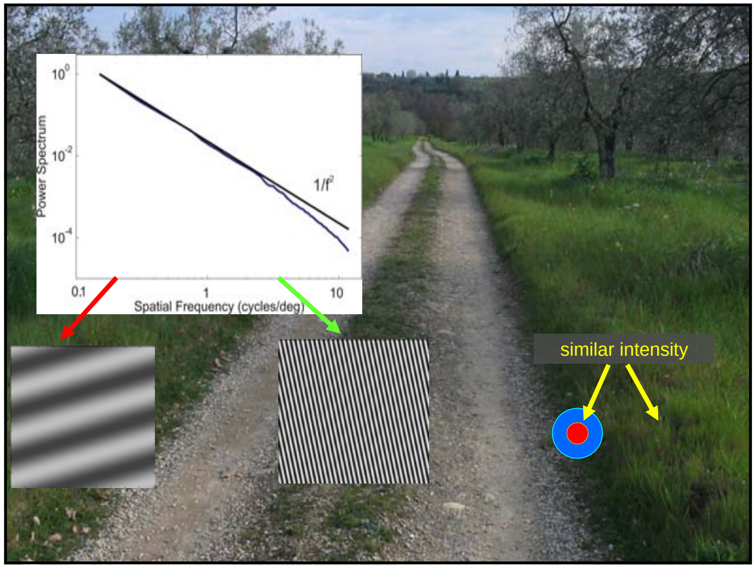
The dynamic decorrelation hypothesis

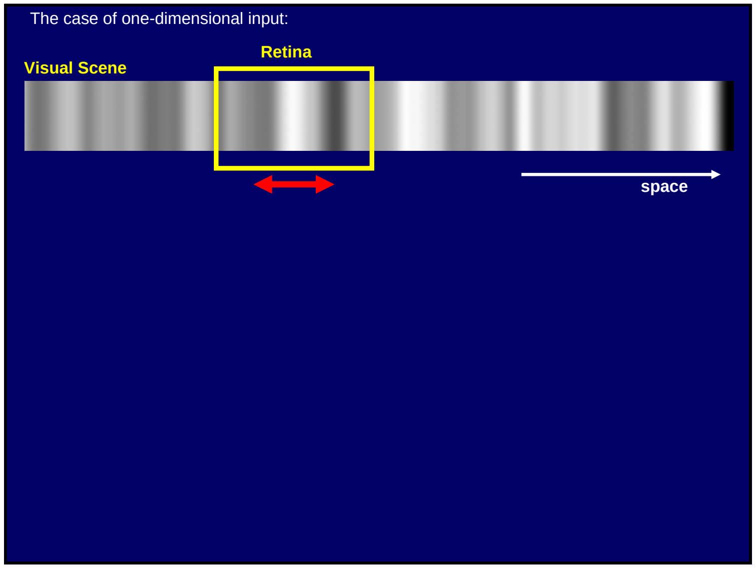
Fixational eye movements are part of a scheme of acquisition of visual information that

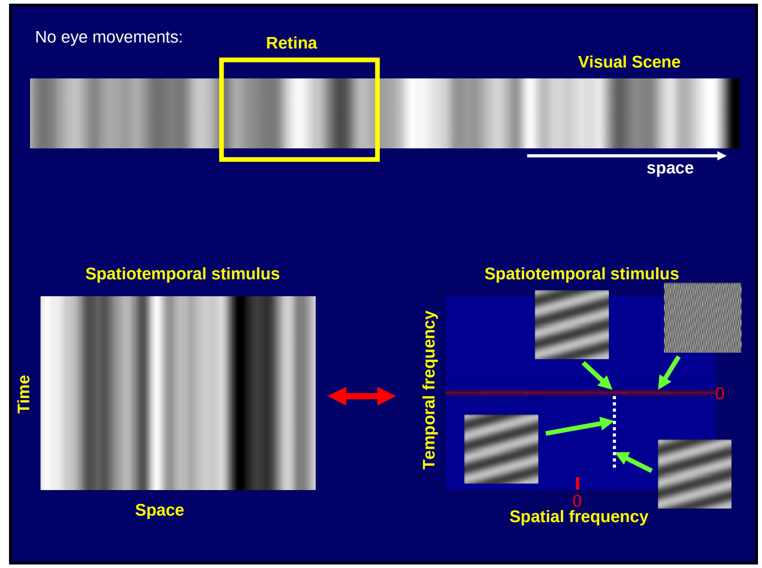
- discards predictable, “uninteresting” correlations present in natural scenes.
- preserves unpredictable, “interesting” correlations.
- emphasizes high spatial frequencies
- is tuned to work with images of our visual world.
- it is similar to mpeg encoding!

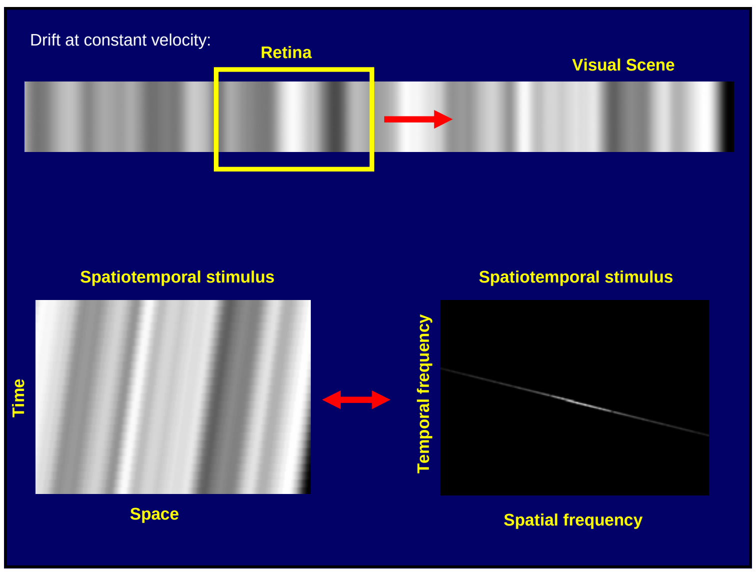


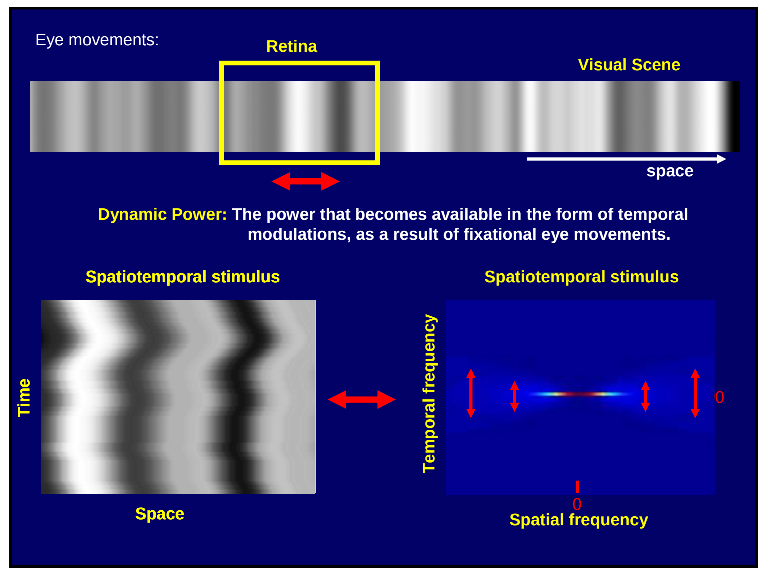


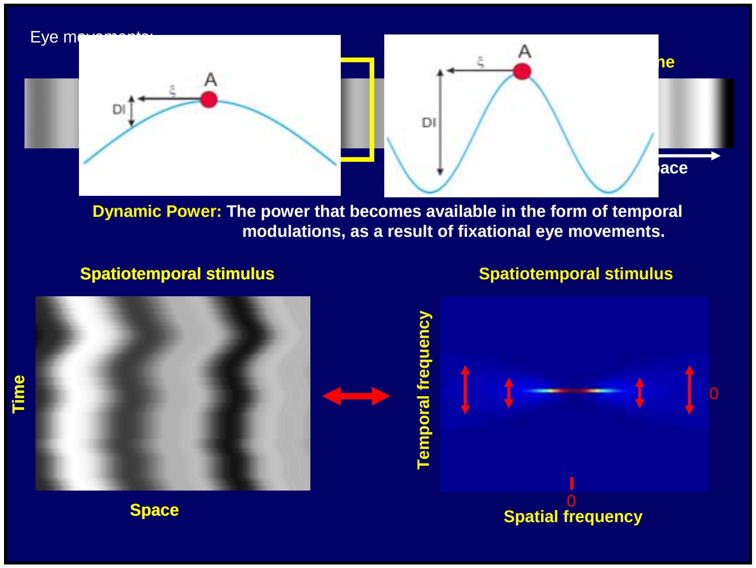



The case of one-dimensional input:
Retina
Visual Scene
space

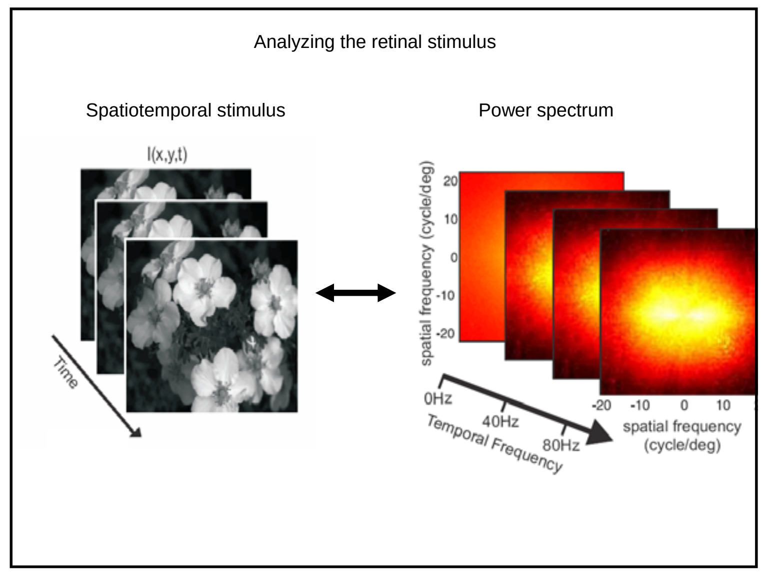

No eye movements:
Retina
Visual Scene
space
Spatiotemporal stimulus
Spatiotemporal stimulus
Time
Space
Temporal frequency
0
0
Spatial frequency

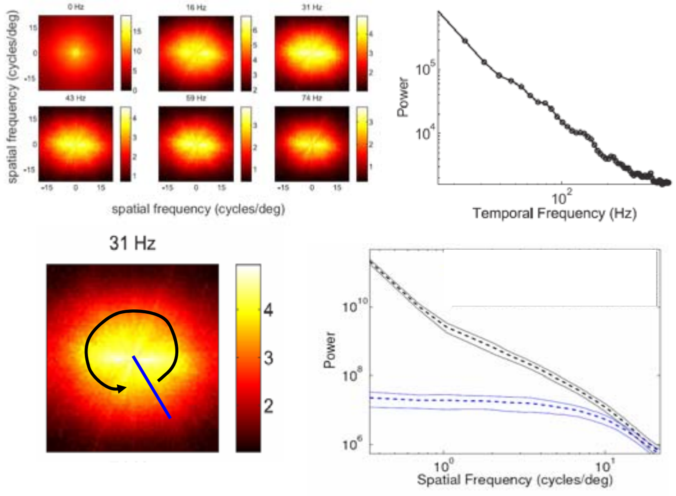

Drift at constant velocity:
Retina
Visual Scene
Spatiotemporal stimulus
Spatiotemporal stimulus
Time
Space
Temporal frequency
Spatial frequency


Eye movements:
Retina
Visual Scene
space
Dynamic Power: The power that becomes available in the form of temporal modulations, as a result of fixational eye movements.
Spatiotemporal stimulus
Spatiotemporal stimulus
Time
Space
Temporal frequency
0
0
Spatial frequency

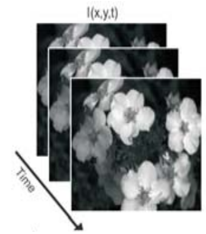

A
DI
A
DI
Dynamic Power: The power that becomes available in the form of temporal modulations, as a result of fixational eye movements.
Spatiotemporal stimulus
Spatiotemporal stimulus
Time
Space
Temporal frequency
0
0
Spatial frequency


What is the stimulus on the retina?

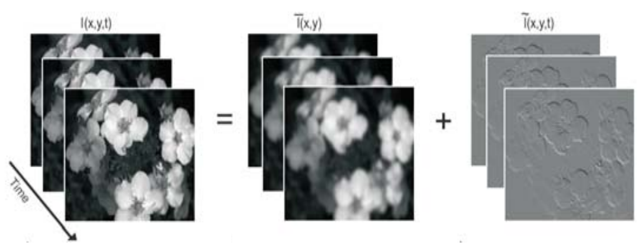

Analyzing the retinal stimulus
Spatiotemporal stimulus
Power spectrum
I(x,y,t)
Time
spatial frequency (cycle/deg)
20
10
0
-10
-20
0Hz
40Hz
80Hz
Temporal Frequency
-20
-10
0
10
spatial frequency (cycle/deg)



Deconstructing the retinal stimulus

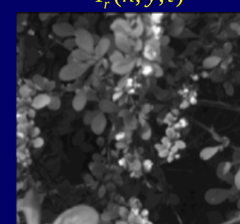


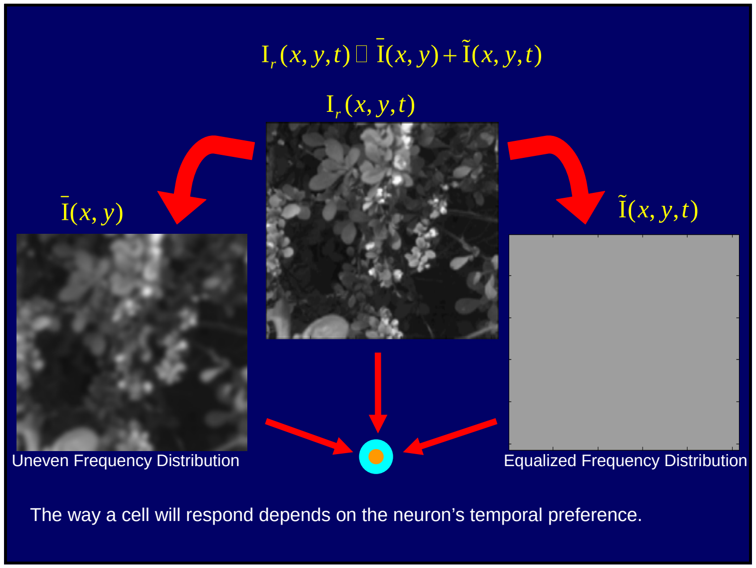
Deconstructing the retinal stimulus

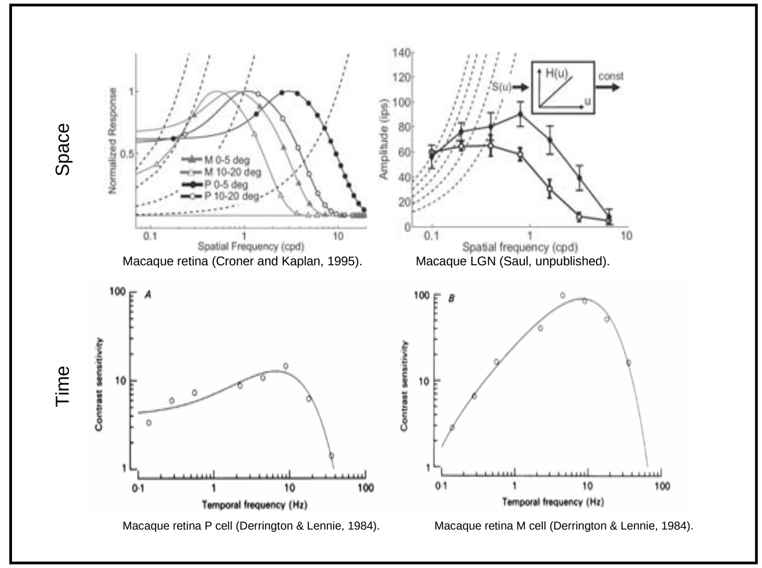


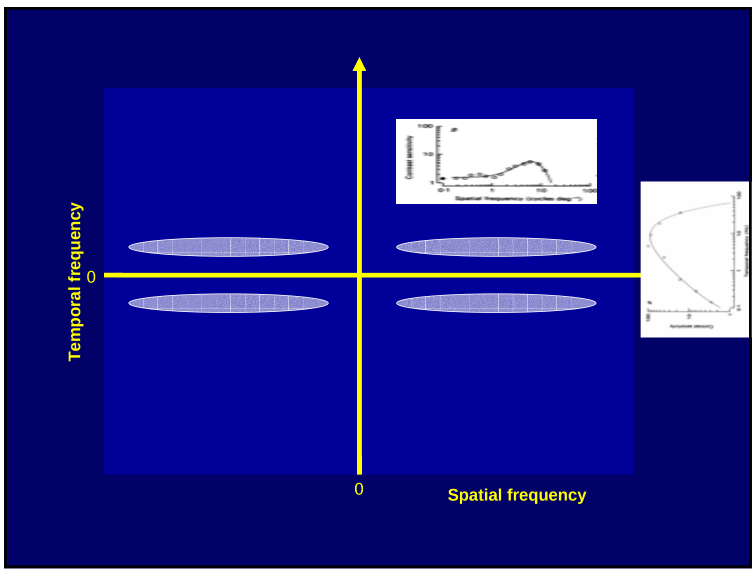
$$\mathrm{I}_r(x,y,t) = \bar{\mathrm{I}}(x,y) + \tilde{\mathrm{I}}(x,y,t)$$

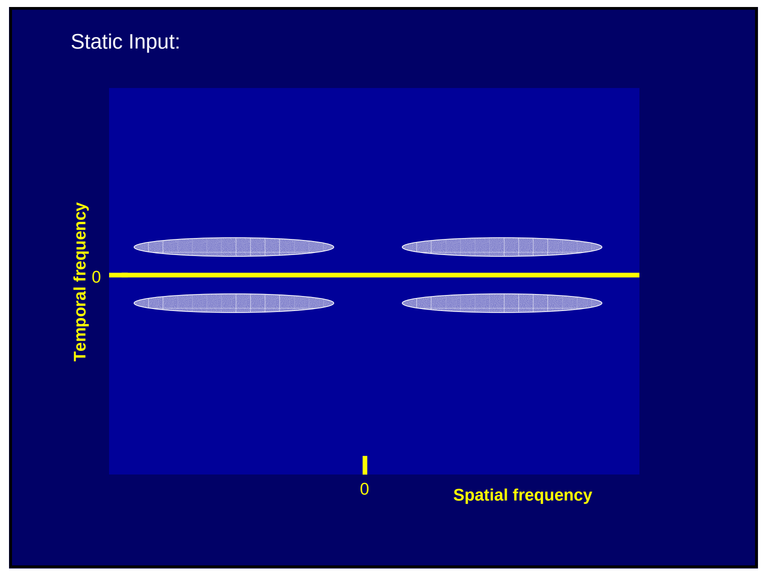
$\mathrm{I}_r(x,y,t)$

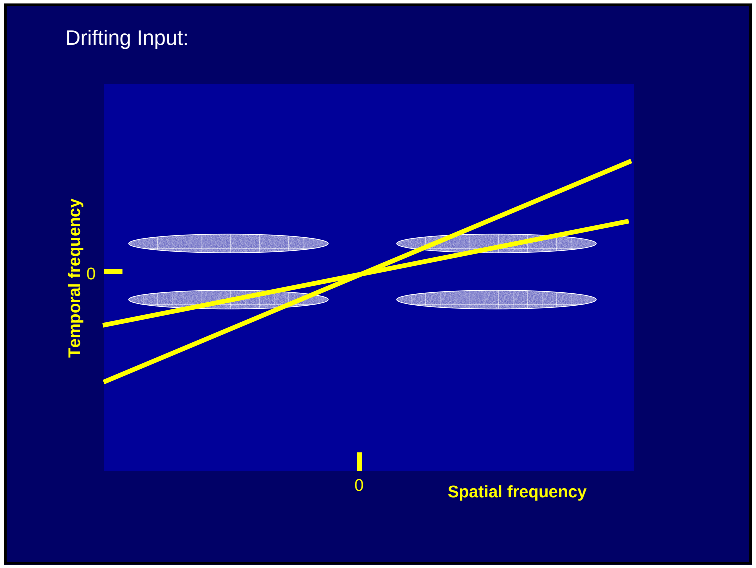


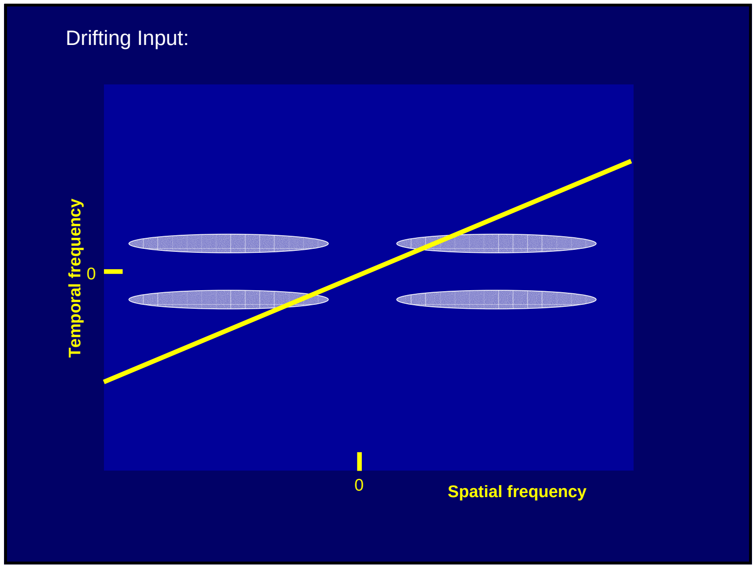

I_r(x,y,t) ≈ Ī(x,y) + Ĩ(x,y,t)
I_r(x,y,t)
Ī(x,y)
Ĩ(x,y,t)
Uneven Frequency Distribution
Equalized Frequency Distribution
The way a cell will respond depends on the neuron's temporal preference.

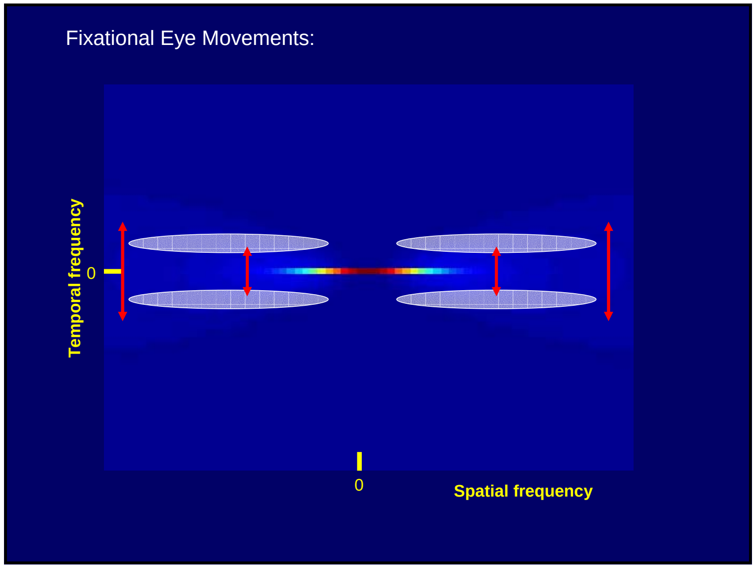

Space
Time
Normalized Response
Spatial Frequency (cpd)
M 0-5 deg
M 10-20 deg
P 0-5 deg
P 10-20 deg
Amplitude (ips)
Spatial frequency (cpd)
H(u)
S(u)
const
Macaque retina (Croner and Kaplan, 1995).
Macaque LGN (Saul, unpublished).
Contrast sensitivity
Temporal frequency (Hz)
Macaque retina P cell (Derrington & Lennie, 1984).
Macaque retina M cell (Derrington & Lennie, 1984).

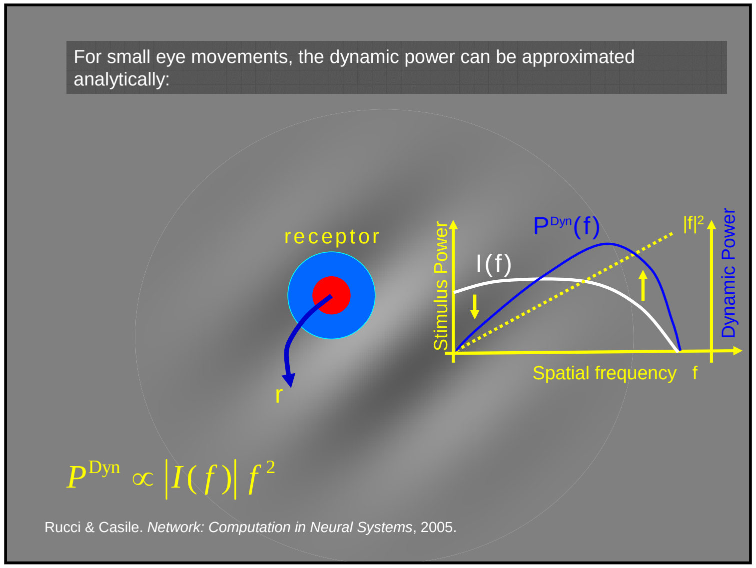

Temporal frequency
0
0
Spatial frequency


Static Input:
Temporal frequency
0
0
Spatial frequency

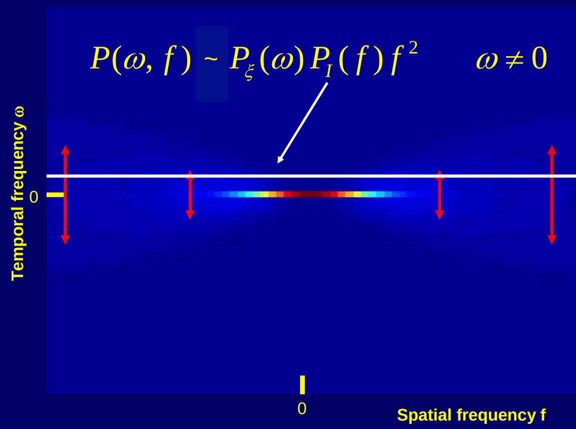

Drifting Input:
Temporal frequency
0
0
Spatial frequency

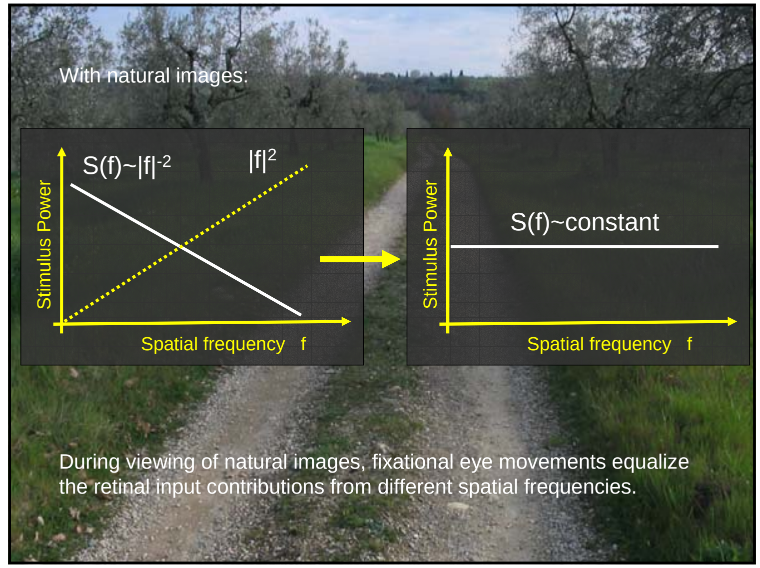

Drifting Input:
Temporal frequency
0
0
Spatial frequency


Fixational Eye Movements:
Temporal frequency
0
0
Spatial frequency

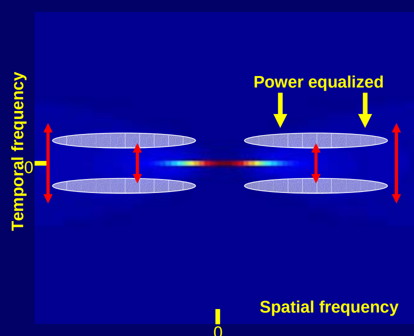

For small eye movements, the dynamic power can be approximated analytically:
receptor
r
Stimulus Power
I(f)
P^Dyn(f)
|f|^2
Dynamic Power
Spatial frequency f
$P^{\mathrm{Dyn}} \propto |I(f)|\, f^2$
Rucci & Casile. Network: Computation in Neural Systems, 2005.

Fixational Eye Movements:





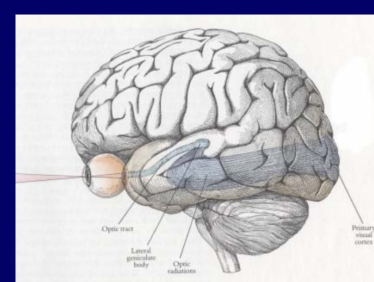
Consequences of equalizing power:



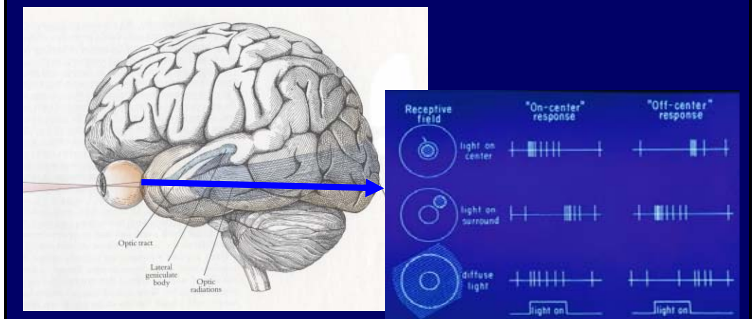
- Neuronal responses to high spatial frequencies are enhanced.
- Responses of pairs of neurons tend to be uncorrelated.

Advantages of equalizing power

- Enhancement to sensitivity to spatial detail.
- Decorrelation in cell responses and more efficient representations.



Spatial Receptive Fields and Neural Decorrelation



The receptive field organization of retinal and LGN neurons eliminates uninteresting correlations due to the general structure of natural scenes
(Srinivasan et al, 1982; Field 1986; Atick and Reidlich, 1992)

Modeling retinal and geniculate neurons

We simulated the responses of retinal and LGN cells by means of spatiotemporal filters:

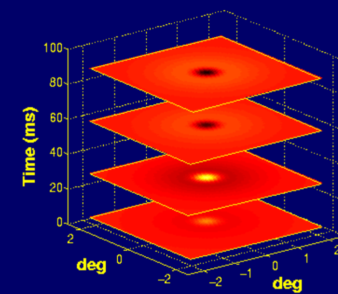
$$I \longrightarrow K \longrightarrow l^{xy}$$

$$l^{xy}(t) = \left[K(x,y,t) \otimes I(x,y,t)\right]_{\theta}$$

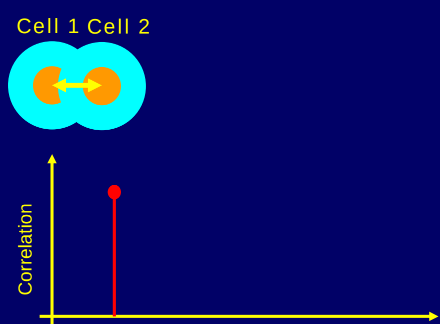
Models are designed on the basis of neurophysiological data.

Spatial RF: Difference of Gaussians.

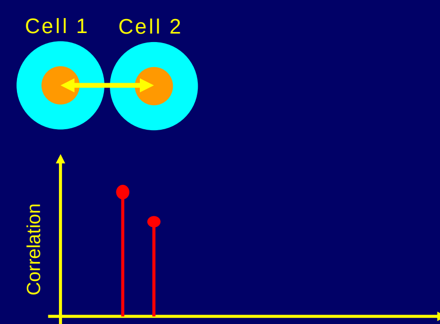
Temporal RF: Biphasic impulse response

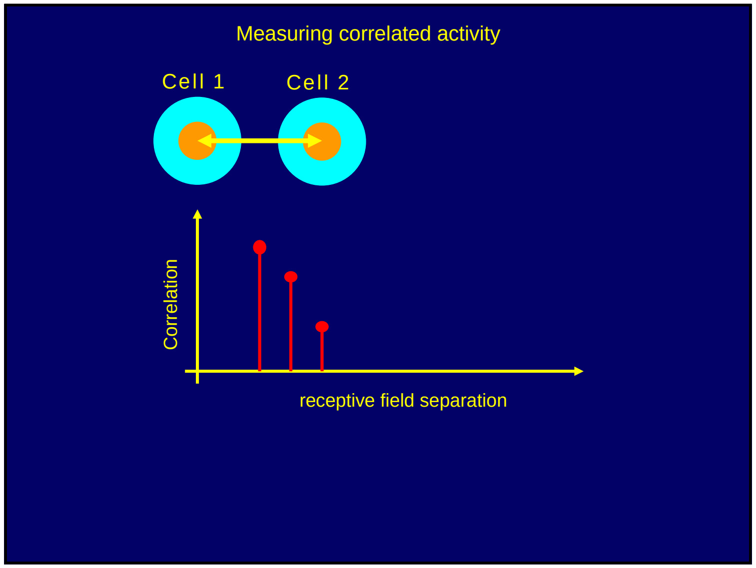


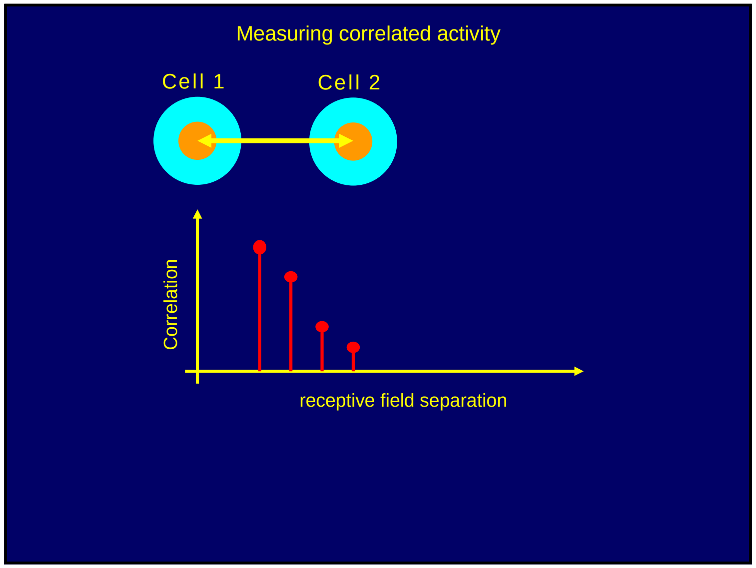
Measuring correlated activity

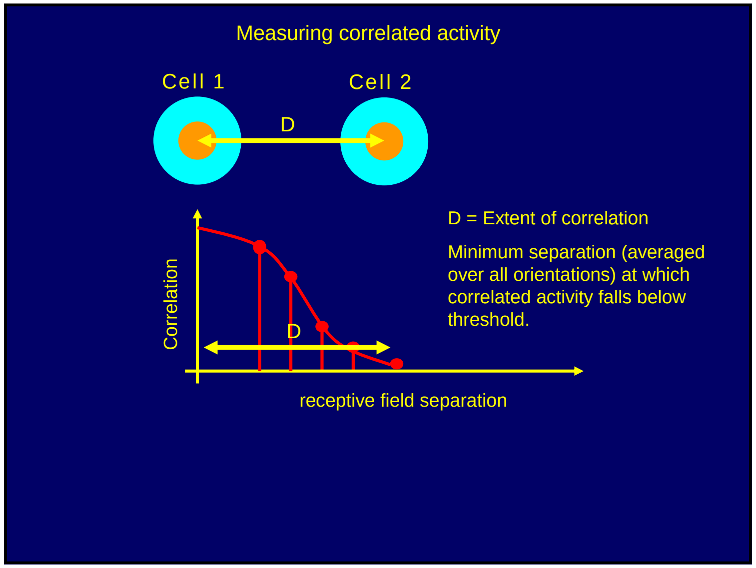


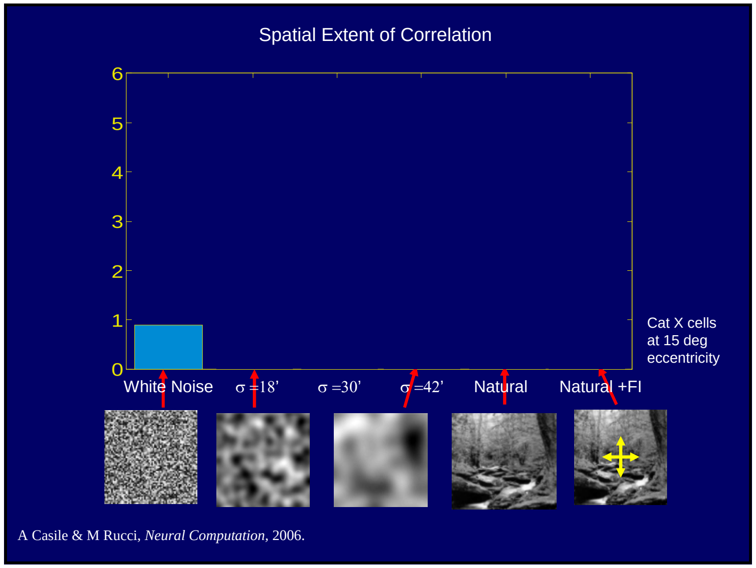
Measuring correlated activity




Measuring correlated activity
Cell 1
Cell 2
Correlation
receptive field separation


Measuring correlated activity
Cell 1
Cell 2
Correlation
receptive field separation


Measuring correlated activity
Cell 1
Cell 2
D
D = Extent of correlation
Minimum separation (averaged over all orientations) at which correlated activity falls below threshold.
Correlation
D
receptive field separation

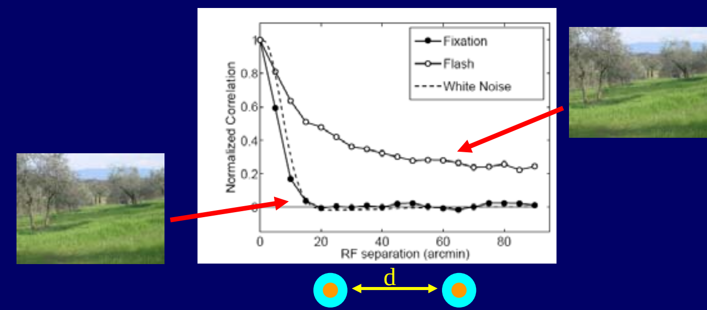

Spatial Extent of Correlation
6
5
4
3
2
1
0
Cat X cells at 15 deg eccentricity
White Noise
σ =18'
σ =30'
σ =42'
Natural
Natural +FI
A Casile & M Rucci, *Neural Computation*, 2006.

Origins of Dynamic Decorrelation

Dynamic decorrelation is a robust phenomenon that results from the interaction of three elements:

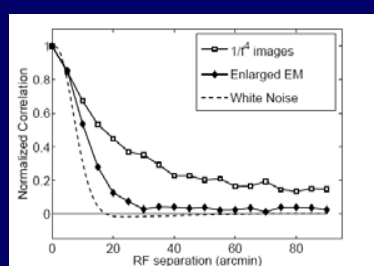
- The statistics of natural images.
- The characteristics of fixational eye movements.
- The dynamics of cell responses.

Models of magnocellular ganglion cells in the primate retina



Rucci, *Network: Computation in Neural Systems*, 2008.

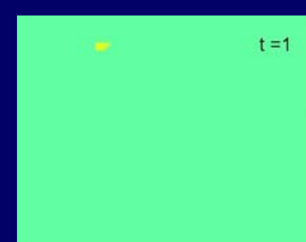
Models of magnocellular ganglion cells in the primate retina



Decorrelation does not occur with non-natural images or with enlarged fixational eye movement.

The spatial decorrelation operated by fixational eye movements does not come at the expense of an increment in temporal correlation.

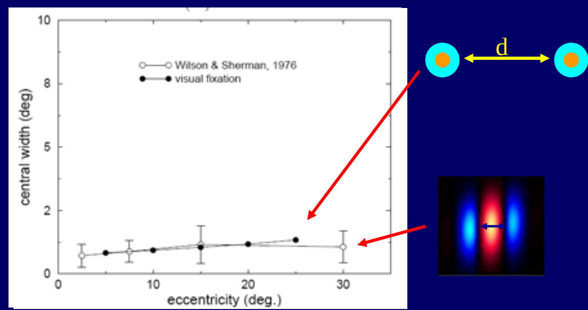
Fixational Eye Movements



Static stimulus presentation

Decorrelation and Visual Development

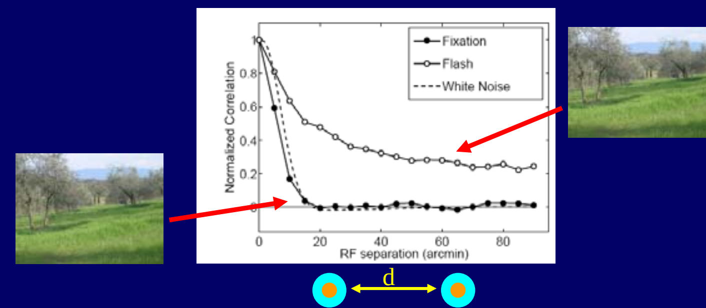
Fixational eye movements might also influence visual development.



Comparison between the width of the main lobe of V1 receptive fields measured in the cat and that predicted by the structure of correlated activity in models. Results at various angles of visual eccentricity are shown.

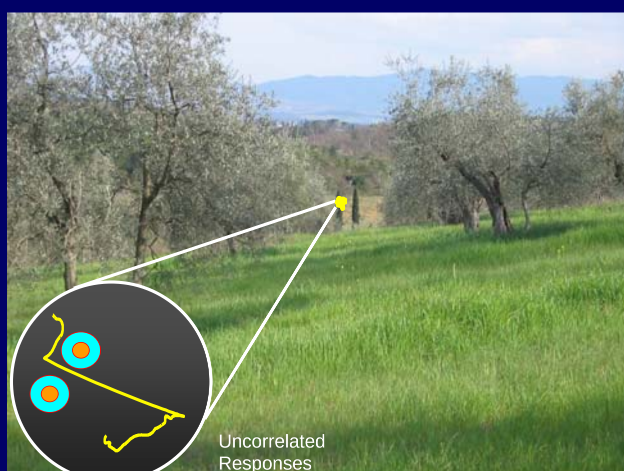
Rucci, Edelman & Wray, Journal of Neuroscience, 2000.
Rucci & Casile, Visual Neuroscience, 2004.

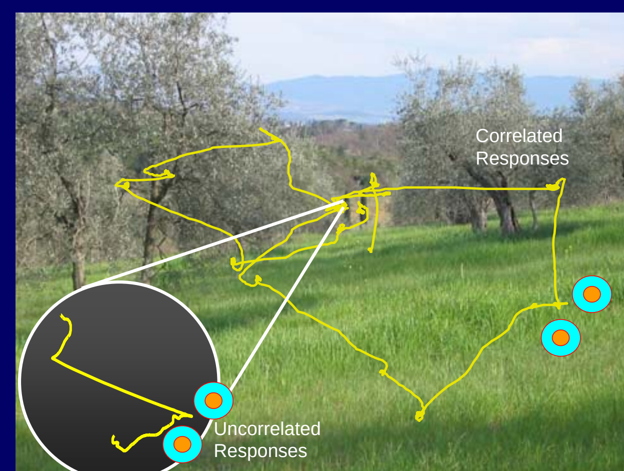
Models of magnocellular ganglion cells in the primate retina



Fixational instability is an effective strategy for viewing natural scenes. It contributes to the establishment of efficient representations with uncorrelated responses.

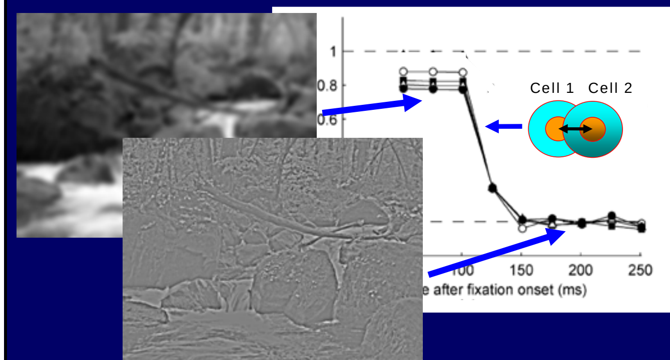
Rucci, *Network: Computation in Neural Systems*, 2008.





Decorrelation occurs progressively during fixation

The natural alternation of macroscopic and microscopic eye movements gives rise to a well-defined dynamics of retinal activity

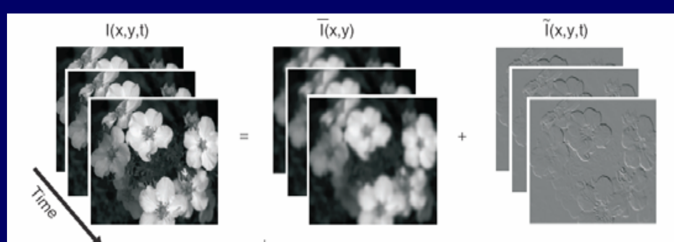


A temporal multiplexing of spatial information!

Desbordes & Rucci, *Visual Neuroscience*, 2007.

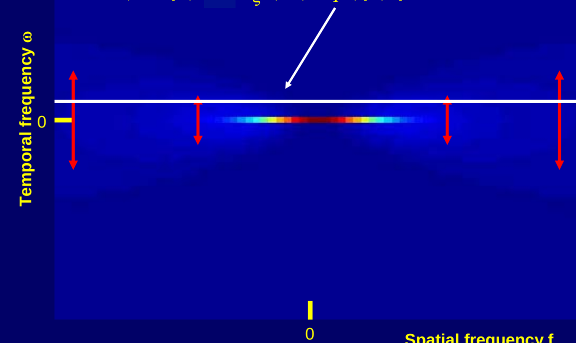
Neural activity during a sequence of eye movements simulated in real-time by means of Piotr Dudek's SCAMP.

How can we test these ideas?



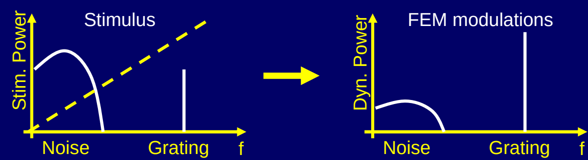
Fixational Eye Movements:

$$P(\omega, f) \sim P_{\xi}(\omega) P_I(f) f^2 \qquad \omega \neq 0$$



Predictions of Dynamic Decorrelation Theory

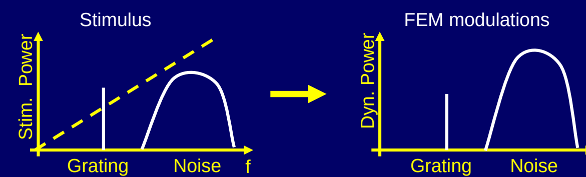
Prediction 1:



Fixational eye movements should improve detection/discrimination of a high-frequency grating masked by low-frequency noise

Predictions of Dynamic Decorrelation Theory

Prediction 2:



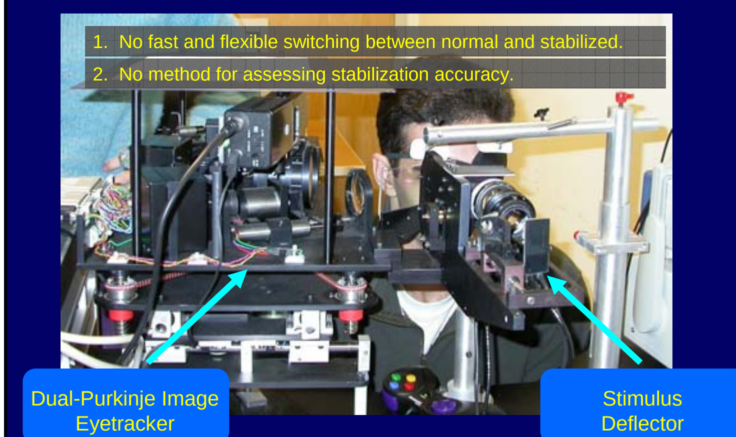
Fixational eye movements should not improve detection/discrimination of a low-frequency grating masked by high-frequency noise

Fixational eye movements and the perception of spatial detail

- Fixational eye movements might contribute to the perception of fine spatial details (Hering, 1899). Dynamic theories of visual acuity (Averill and Weymouth, 1925, Marshall and Talbot, 1942).

However, classical experiments that eliminated retinal image motion did not support these theories:

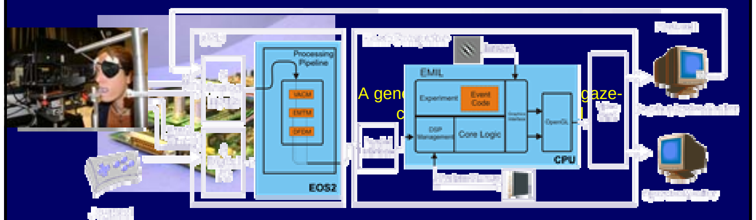
- Long stimulus durations: global reduction in contrast sensitivity, more pronounced at low –rather than high– spatial frequencies (Koenderink, 1972; Kelly, 1979).
- Brief stimulus durations: little or no effect of image stabilization on visual acuity and contrast sensitivity (Riggs et al 1953; Tulunay-Keesey and Jones, 1976).



Rucci and Desbordes, *Journal of Vision*, 2003.

Flexible retinal stabilization

New technique of retinal stabilization based on real-time processing of eye-movement signals

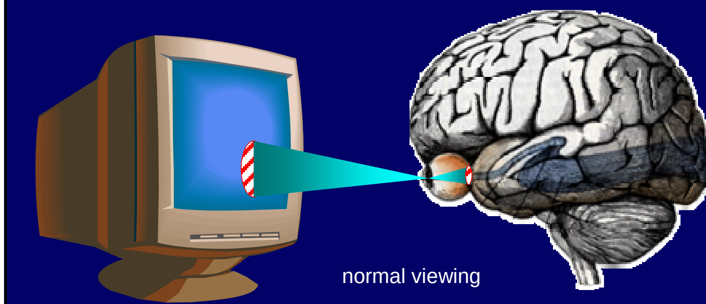


EyeRIS guarantees refresh of the stimulus with a maximum delay equal to two frames on the CRT display (10 ms at 200 Hz, typical delay 7.5 ms).

Santini, Redner, Iovin & Rucci, *Behavioral Research Methods*, 2007.

Retinal Stabilization via Eye-Movement Contingent Display (EMCD) Control

EMCD control enables accurate control of the position and motion of the stimulus on the retina.



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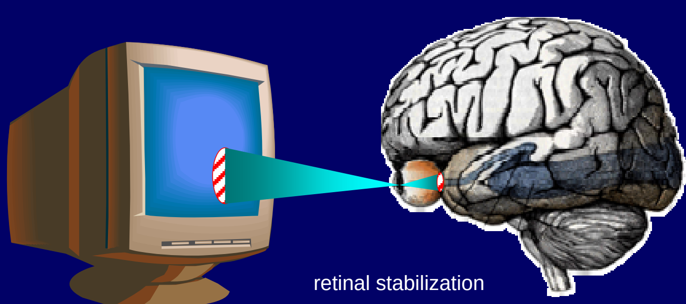


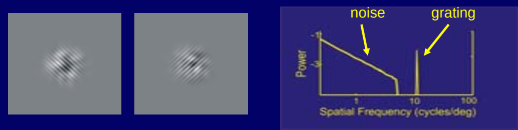
EyeRIS: A system for flexible EMCD control

1. Intersaccadic stabilization.
2. Randomly alternating trials.
3. Evaluation of stabilization accuracy.

Psychophysical Experiments: Task and Stimuli

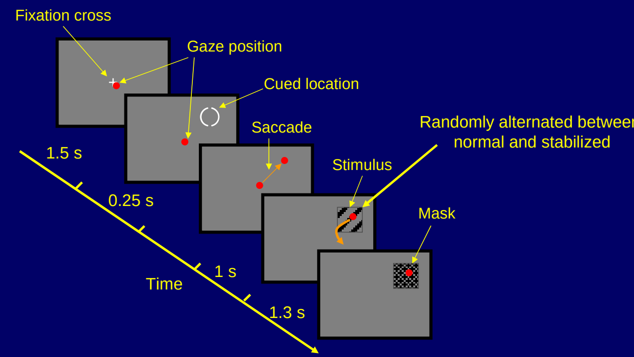
Subjects reported whether a grating was tilted by 45º clockwise or counter-clockwise.

Experiment 1 (High Frequency) 11 cycles/deg grating + 1/f noise below 4 cycles/deg

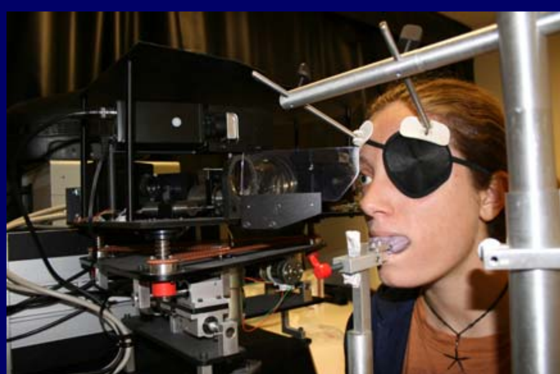


Experiment 2 (Low Frequency) 4 cycles/deg grating + 1/f noise above 10 cycles/deg

Procedure



We compared discrimination performances measured in two conditions: in the presence or absence of the retinal image motion produced by fixational eye movements.



Experiment 1

High-frequency grating + Low-pass 1/f noise

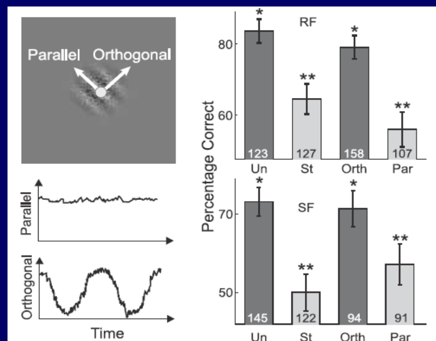
Experiment 2

Low-frequency grating + High-pass 1/f noise

FEM improved discrimination of the orientation of a high-frequency grating masked by low-frequency noise (Experiment 1) but did not help with a low-frequency grating masked by high-frequency noise (Experiment 2).

Rucci, Iovin, Poletti, and Santini, *Nature* 2007.

Limiting Retinal Image Motion to a Single Axis

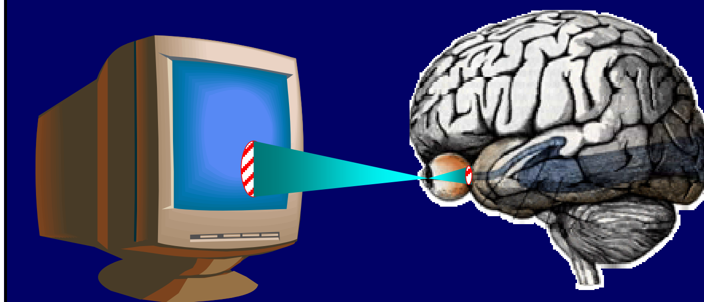


Discrimination is impaired when fixational input modulations do not convey information about the grating. Conversely, performance is normal when these input modulations contain information about the grating's orientation.

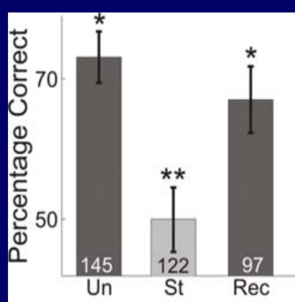
Rucci, Iovin, Poletti, and Santini, *Nature* 2007.

Active vs. Passive Exposure to Retinal Image Motion

A **stabilized** stimulus moves on the monitor in a way that recreates the normal fixational motion of the retinal image.



Active vs. Passive Exposure to Retinal Image Motion



Passive exposure to the fixational motion of the retinal image is sufficient for reestablishing a normal level of performance.

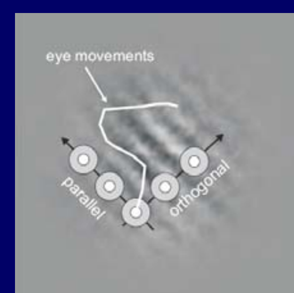
(*) Conditions statistically different from Stabilized.

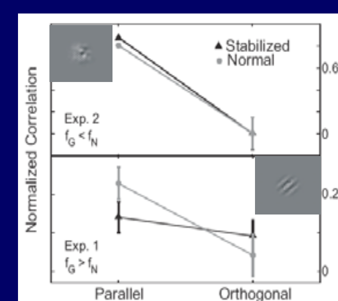
(**) Conditions statistically different from Unstabilized.

Performance is normal when input modulations contain information about the grating's orientation, independent of whether the subject actively produced retinal image motion by means of fixational eye movements or was passively exposed to it under conditions of retinal stabilization.

Modeling Experimental Trials

Models of parvocellular ganglion cells were stimulated by input signals that replicated the visual input experienced by subjects in the experiments.





The degree of synchronization in neuronal responses predicts psychophysical performance.

Poletti & Rucci, Journal of Vision, 2008.

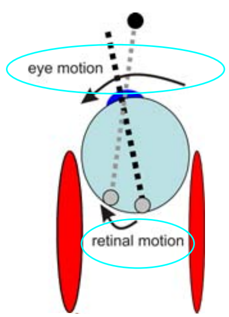
Why don't we see the retinal motion caused by fixational eye movements?

Extraretinal vs. **Retinal** Theories

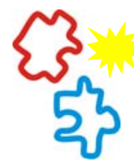
An *afferent copy* of the oculomotor command is used to compensate for retinal motion due to eye movements!

Self-motion is estimated from changes in the retinal image (*visual kinesthesis*)!

Decoupling the retinal and extraretinal signals

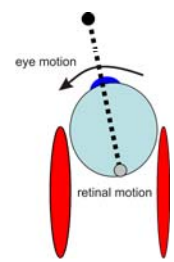


Under natural viewing, the possible contributions of retinal and extraretinal mechanisms cannot be easily disentangled



Retinal Stabilization

How do you perceive a dot that moves with your eyes?

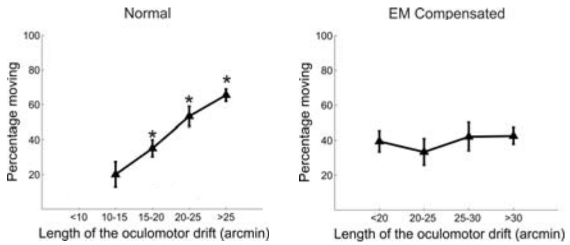


EXTRARETINAL THEORIES:
The dot is moving!

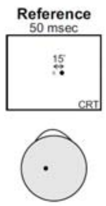
RETINAL THEORIES:
The dot is stationary!

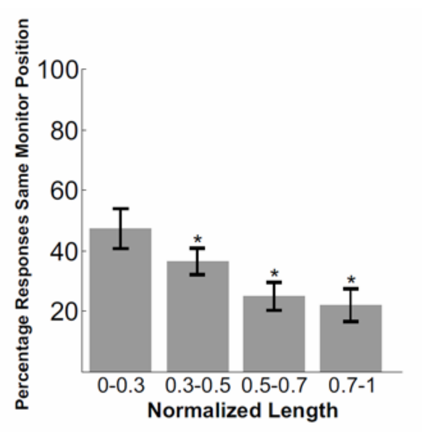
Retinal Stabilization decouples retinal and extraretinal signals

Cancellation of ocular drift does not rely on an extraretinal signal



Poletti and Rucci, under review.





Poletti and Rucci, under review.